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Aspects of the Reproduction of Rocky Intertidal Mollusks from the Jordan Gulf of Aqaba (Red Sea)

by

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Abstract. Reproductive and spawning periodicity, type of spawn, and spawning behavior of an intertidal chiton, 11 prosobranch gastropods, and one pulmonate gastropod, and two pelecypods from the Jordan Gulf of Aqaba are given. Reproduction was continuous in seven species, restricted to the warmer period and lowered sea level in seven, and in one species occurred during the colder and higher sea level period. No direct relationship between temporal reproduction and tide level or vertical position in the intertidal zone was seen.

INTRODUCTION

THE LITTLE INFORMATION available on the fauna of the rocky intertidal of the Red Sea, including the Gulf of Aqaba, is concerned primarily with zonation (SAFRIEL & LIPKIN, 1964; FISHELSON, 1971; AYAL & SAFRIEL, 1980; SAFRIEL *et al.,* 1980). SAFRIEL (1969) reported on various aspects of the ecology of *Nerita* spp. and JORNÉ & SAFRIEL (1979) on the behavior of *Nerita polita* Linnaeus. Data on the reproduction of Red Sea intertidal mollusks are lacking except for very limited data given by SAFRIEL (1969) on *Nerita polita* and FAO (1972) on *Ostrea forskali* Chemnitz.

Various aspects of the reproduction of 15 intertidal mollusks from the Jordan coast of the Gulf of Aqaba have been investigated. The aspects include reproductive and spawning periodicity, type of spawn, and spawning behavior. The relationships of these to external environmental factors including position in the intertidal zone, temperature, changes in sea level, and primary production are discussed.

MATERIALS AND METHODS

A minimum of 10 specimens of each species was collected around the middle of each month for at least 12 months. The species were usually collected from the same locality each month, in some cases from two different localities. Collections were spatially random but biased toward larger sizes to ensure obtaining sexually mature individuals. An investigation of the minimum size of sexual maturity of most species was conducted.

In the laboratory, specimen length was measured to the nearest 0.1 mm using vernier calipers; microscopic measurements to the nearest 0.01 mm were made with an ocular micrometer.

The shells of the gastropods were cracked using a hammer, those of the bivalves opened, the foot of the chiton removed, and the whole animal of limpets removed to examine the gonads under a dissecting microscope. Either teasing or microdissection of the gonads and/or associated structures was employed to determine the presence or absence of gametes. When necessary, fresh preparations were examined under a compound microscope.

Additional investigations including ones on the deposition of eggs and hatching were conducted in the laboratory for some of the species. Specimens were kept in individual aerated seawater aquaria.

The terminology used for the zones in the rocky intertidal is that of STEPHENSON & STEPHENSON (1949) and SAFRIEL & LIPKIN (1964). The littorinid zone of Safriel & Lipkin is within the supralittoral fringe of Stephenson & Stephenson; the chthamalid and *Tetraclita* zones of Safriel & Lipkin are within the midlittoral zone of the Stephensons. FISHELSON (1971) included the entire rocky intertidal of the Red Sea in the infralittoral and referred to it as the *Tectarius armatus-Tetraclita squamosa rufotincta* community.

Adult specimens of all 15 species studied as well as egg capsules, masses, and ribbons are deposited in the reference collection of the Marine Science Station, Aqaba, Jordan, and are available for examination upon request. In addition, voucher specimens of all species have been deposited in the Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C.

DESCRIPTION OF THE ROCKY INTERTIDAL ZONE

The region of the Jordan Gulf of Aqaba is within the very warm portion of the Saharan bioclimatic zone. The terrestrial component exerts greater influences on the intertidal and shallow marine zones than vice versa. The greater influences are due to the limited areal extent of the Gulf with respect to the surrounding terrestrial area, a narrow and clear-cut interface between the terrestrial and marine environments, land-to-Gulf hot and dry winds reducing transport of moisture in the opposite direction, and low rainfall.

The prevailing winds are N-NNE, with Beauforts 2 through 4 occurring 84% of the time (HULINGS, 1979). Mean air temperatures range from about 16°C in January to 32°C in August (Jordan Meterological Department) and surface water temperatures from 20°C in February to 27°C in August–September (MORCOS, 1970). In the absence of river runoff and in combination with low rainfall (35 mm/yr, Jordan Meterological Department) and dry and hot winds, the evaporation rate is high (up to 4 m/yr, ANATI, 1976) resulting in high, constant salinity of 40.5 to 41.0 ppt (PALDOR & ANATI, 1979). There is a major period of primary productivity during December–January and a minor period during May–June (HULINGS & ABU HILAL, 1983). LEVANON-SPANIER *et al.* (1979) consider the northern Gulf of Aqaba to be oligotrophic from April through November.

According to MORCOS (1970) the tides of the Gulf of Aqaba are influenced by those of the Red Sea proper and the direct effects of the moon and sun are comparatively small. In addition, the tides are usually out of phase with the moon (Hulings, unpublished data). The tide in the Jordan Gulf is mixed, with diurnal inequality of the highs averaging 4.2 cm and that of the lows 4.7 cm (Hulings, unpublished data). The spring tide range averages about 1.0 m, the range of the neaps about 50 cm (FISHELSON, 1973; Hulings, unpublished data). Fluctuation of sea level, up to 1 m, occurs annually, being higher during the period December through May and lower from July through October (FISHELSON, 1973; Hulings, unpublished data). Although the vertical ranges and variations in tides are small, the net effect of the level and duration of submergence and emergence on the generally low profile beaches is considerable.

The substratum of the rocky intertidal includes boulders (ranging from granitic to huge masses of conglomerate or fossil reef), mostly medium to large-sized granitic and dike multi-colored pebbles underlain by sand, and platform or slab. The latter is extremely variable and includes sandstone, conglomerate (calcium carbonate cemented sand, gravel, and pebble mixtures) and beach rock (usually gravel sized and continuously forming). Eroded fossil coral reefs, composed mostly of a variety of coral heads surrounded by solidified calcium carbonate detritus (FRIEDMAN, 1965), are also included as part of the slab substrata or platform beaches. It is common to find mixtures of two or more of the slab substrata at any particular locality. The horizontal profile of the slab beaches is generally very gentle, whereas that of the pebble beaches is somewhat steeper. In addition, wave action is minimal on the usually protected slab beaches and moderate on the more exposed pebble beaches.

ASPECTS OF REPRODUCTION

Class Polyplacophora

Family CHITONIDAE

Acanthopleura haddoni Winkworth, 1927

Habitat: Most common in the *Tetraclita* (midlittoral) zone.

Specimens examined: 375 averaging 50 mm long from June 1982 through May 1984 for state of reproduction; 39 specimens 16–42 mm long for minimum length at which gonads appear.

Sex ratio: 1.0 male:0.8 female.

Reproduction: The testes are dark red when immature, pinkish when mature; immature ovaries are tan, mature ovaries dark to black brown. Gametes were present in both sexes from June through December. Among the females, all were ovigerous from September through November; during other months, ovigerous and nonovigerous individuals occurred. Ova with a chorion (KUMÉ & KATSUMA, 1957) were found from August through November. The majority of the males had enlarged testes with sperm from June through October. The major period of reproduction (the time that most specimens of both sexes had gametes) is from June through October.

The smallest female with ovaries was 24 mm long, the smallest male with testes 27 mm long.

Class Gastropoda, subclass Prosobranchia

Family PATELLIDAE

Cellana radiata (Born, 1778)

Nomenclature: According to Dr. J. Rosewater (personal communication), *Cellana radiata* is synonymous with and has priority over *C. rota* (Gmelin, 1791) reported by SAFRIEL & LIPKIN (1964), FISHELSON (1971), MERGNER & SCHUHMACHER (1974), and MASTALLER (1979).

Habitat: Characteristic of the *Tetraclita* (midlittoral) zone.

Specimens examined: 597 averaging 33.0 mm long (range, 16.7–48.0) from March 1982 through May 1984 for state of reproduction; 129 specimens 3.6–23.5 mm long for minimum length with gonads.

Sex ratio: 1.0 male:1.0 female.

Reproduction: Gametes were present in most individuals of both sexes each month. The smallest male was 9.5 mm long, the smallest female 12.0 mm; the smallest male with sperm was 10.2 mm long, the smallest female with ova 12.0 mm long.

Comments: Rao (1973) reported a sex ratio of 1.0 male: 0.8 female in *Cellana radiata* from tropical southeast India. Developing or spawning gonads were present each month during a 12-month period with spawning occurring from June to February or March. Sexual maturity occurred at a length of 9 mm, and sex distinction could be made in individuals 10 mm long. Rao (1976) later reported continuous breeding in *C. radiata* and sexual maturity at a shell length of 10–15 mm.

Family Trochidae

Monodonta dama (Philippi, 1848)

Habitat: A mobile midlittoral species ranging from above the chthamalid zone to the *Tetraclita* (midlittoral) zone.

Specimens examined: 296 from April 1982 through May 1983 for state of reproduction; 62 specimens 5.7–12.3 mm high for minimum size with gonads.

Sex ratio: 1.0 male: 1.1 female.

Reproduction: Dark green ovaries with ova and cream-colored testes with sperm occurred each month. The smallest male with testes was 8.1 mm long, the smallest female with ovaries 9.0 mm long and was ovigerous.

Spawn: Spawning was observed on several occasions in a seawater table with continuously circulating seawater. Most spawning individuals were paired or in clusters, and masses of gametes were released in spurts by both sexes. The ova, averaging 0.13 mm in diameter, were surrounded by a membrane averaging 0.15 mm in diameter. Spawning occurred irrespective of lunar or tidal cycles.

Early development: Veligers averaging 0.19 mm long and lacking eyes and an operculum appeared within 24 h after spawning.

Family Neritidae

Nerita forskalii Recluz, 1844

Nomenclature: This species has been reported from the Jordan Gulf of Aqaba as *Nerita sanguinolenta* Menke, 1820, by Mergner & Schuhmacher (1974) and *N. albicilla* Linnaeus, 1758, by Mastaller (1979). Safriel (1969) noted that the species is *N. forskalii* based on shell morphology.

Habitat: Has a wide vertical distribution on a variety of solid substrata and in varied microhabitats, including tide pools, on pebble beaches, and slab, within the *Tetraclita* (midlittoral) zone. Occurs lower than the other of the sympatric pair, *Nerita polita* Linnaeus.

Specimens examined: 350 averaging 18.4 mm long (range, 7.7–24.8) from April 1982 through May 1983 for reproductive state; 41 specimens 5.9–11.6 mm long for presence of gonads.

Sex ratio: 1.0 male: 1.1 female.

Reproduction: Ova and spermatophores, the latter averaging 6.3/female (range, 0–16), and sperm were present in the seminal vesicle (Berry *et al.*, 1973) each month. The smallest male with testes was 7.7 mm long, the smallest female with ovaries 8.7 mm long.

Copulation was observed in the field every month except August and September and occurred only during submergence. The copulating behavior and the action of the cephalic penis were essentially the same as that described by Iriki *et al.* (1963). Spermatophores were occasionally found in aquaria indicating unsuccessful copulation.

Spawn: The egg capsules have the basic structure described by Andrews (1935). They are reddish brown in color and the presence of the irregular shaped, dark red spherulites give the capsules a faceted appearance. The capsules are more elliptical than round, averaging 2.2 mm wide × 2.8 mm long.

Egg capsule deposition was noted during July, October, and January through May; there were no observations during the other months. The capsules were found on a wide variety of exposed surfaces including glass, metal, shells of other gastropods (living and dead), and the girdle of chitons, as well as on rocky surfaces from small pebbles to slab. The deposition of capsules on a wide variety of surfaces coincides with its wide-ranging distribution and the fact that it usually does not go into hiding during emergence.

Early development: Various stages of embryonic development from uncleaved ova, averaging 0.15 mm in diameter, to veligers with eyes, averaging 0.20 mm long, were found enclosed within the membrane that lined the capsule. The average number of ova–veligers per capsule was 117 (range, 60–211).

Hatched veligers with eyes and operculum averaged 0.21 mm long. Exit of the veligers from the capsule appeared to be through the top.

Nerita polita Linnaeus, 1758

Habitat: Occurs above *Nerita forskalii* in the midlittoral, approximately equivalent to the chthamalid zone and is restricted to areas of pebbles underlain by sand.

Specimens examined: 347 averaging 17.7 mm long (range, 9.0–22.8) from April 1982 through May 1983 for state of reproduction; 24 specimens 5.7–11.0 mm long for minimum size with gonads.

Sex ratio: 1.0 male: 1.4 female.

Reproduction: Ova and spermatophores (the latter averaged 5.8/female, range, 0–20) and sperm in the seminal

vesicle (Berry *et al.*, 1973) were present each month. The smallest male with testes was 8.0 mm long, the smallest female with ovaries 9.6 mm long.

Copulation was observed in the field from May through July and September through March and was essentially like that described by Iriki *et al.* (1963) in terms of the behavior and action of the cephalic penis. Copulation occurred only among emergent pairs and during day and night. Safriel (1969) and Hughes (1971) reported copulation in *Nerita polita* from May through the beginning of August during investigations from April through the beginning of August.

Spawn: The egg capsules, having the basic structure described by Andrews (1935), are white due primarily to the irregular and small spherulites, and have a finely granulated appearance. They are circular, averaging 1.7 mm in diameter. The average number of ova–veligers per capsule was 35 (range, 22–55).

Capsule deposition was noted from May through July and during December; deposition is, however, probably more frequent. The capsules are deposited in groups on the sides of large pebbles that are well-anchored in the sand. Deposition is always beneath the surface of the sand and on relatively smooth surfaces. The site of deposition is in keeping with the snail's behavior of burrowing into sand and attaching, by means of the foot, to the sides of pebbles during maximum ebb and maximum flood tides. Emergence occurs during flooding and ebbing tides during day and night. Variable patterns of behavior in *Nerita polita,* ranging from primarily nocturnal (Safriel, 1969; Hughes, 1971) to no nocturnal activity (Zann, 1973), have been reported.

Early development: Uncleaved ova, averaging 0.19 mm in diameter, through veligers, averaging 0.25 mm long, with eyes and an operculum were observed enclosed in the membranous lining of the capsule. Veligers apparently leave the capsule near the base. Hatched veligers averaged 0.25 mm long and were kept alive for 14 d, during which no significant morphological changes occurred.

Family Littorinidae

Littorina scabra scabra (Linnaeus, 1758)

Nomenclature: According to Dr. J. Rosewater (personal communication) the species and subspecies names are provisional, pending the publication of a revision by Dr. D. Reid.

Habitat: Found at only one locality, on boulders in the main port of Aqaba. It occurred in the transitional littorinid–chthamalid (supralittoral fringe–midlittoral) zones from May 1982 through January 1983.

Specimens examined: 61 averaging 12.6 mm long (range, 7.2–18.1).

Sex ratio: 1.0 male:1.3 female.

Reproduction: The ovoviviparous females were ovigerous and the males contained sperm in the vas deferens each month.

Early development: The ctenidial brood pouch (Rosewater, 1970) contained various stages of development during each month except September and January. The stages ranged from early cleavage to free, eyeless veligers averaging 0.11 mm long.

Nodilittorina millegrana (Philippi, 1848)

Nomenclature: Rosewater (1970) states that *Littorina novaezelandiae* Reeve, 1857, reported by Safriel & Lipkin (1964) and *Littorina urieli* described by Biggs (1966) from Eilat, Israel, are synonyms of *Nodilittorina millegrana.*

Habitat: Characteristic of the littorinid (supralittoral fringe) zone and most common on near vertical surfaces of boulders. It is the second highest mollusk in vertical distribution in the rocky intertidal zone.

Specimens examined: 371 averaging 9.0 mm long (range, 3.2–14.3) from April 1982 through May 1983 for reproductive state; 270 specimens 1.0–6.5 mm long for minimum size of sexual maturity.

Sex ratio: 1.0 male:1.7 female.

Reproduction: Males with sperm in the vas deferens and females with ova in the oviduct were found each month. The smallest male possessing a rudimentary penis was 2.5 mm long and the smallest with a fully developed penis and sperm in the vas deferens was 3.3 mm. The smallest ovigerous female was 4.1 mm long.

Spawn: *Nodilittorina millegrana* produces pelagic egg capsules. Each capsule contains a single egg, is transparent and dome-shaped, being flattened on one side and elevated on the opposite in three tiers (two rings) (Tokioka & Habe, 1953; Rosewater, 1970). The capsules averaged 0.19 mm in diameter and 0.08 mm in height. The area containing the egg averaged 0.08 mm in diameter.

Early development: Based on observations of capsules isolated in culture dishes, the development from zygote (average, 0.07 mm in diameter) into the veliger stage occurred within about 24 h. During the next 24 h, veligers having an operculum but lacking eyes left the capsule via a torn area on the flattened side. Veligers remained alive for 5 d following hatching and averaged 0.13 mm long. Neither eyes nor any other major morphological feature developed during this period.

Nodilittorina subnodosa (Philippi, 1847)

Nomenclature: What Safriel & Lipkin (1964) reported as *Tectarius armatus* Issel from the littorinid zone at Eilat, Israel, and Fishelson (1971) reported is *Nodilittorina subnodosa.* According to Dr. J. Rosewater (personal com-

munication), *T. armatus* appears to be a fossil and is probably a trochid.

Habitat: The highest occurring mollusk in the rocky intertidal zone and characteristic of the upper littorinid (supralittoral fringe) zone. It is most common on nearly horizontal slab substrata.

Specimens examined: 339 averaging 9.0 mm long (range, 4.3–13.2) from May 1982 through May 1983 for state of reproduction; 112 specimens 2.2–5.0 mm long for minimum size of sexual maturity.

Sex ratio: 1.0 male:2.1 female.

Reproduction: All females contained ova in the oviduct and all males had sperm in the vas deferens from June through September. Females with and without ova and males with and without sperm were found in May and October. The major period of reproduction is considered to be June through September. From October through April there was no noticeable degeneration in the size of the penis, as PALANT & FISHELSON (1968) saw during the non-reproductive period of *Littorina neritoides* (Linnaeus, 1758).

The smallest male having a recognizable, rudimentary penis was 2.4 mm long and the smallest male with a fully developed penis and sperm in the vas deferens was 3.4 mm. The smallest ovigerous female was 4.1 mm long.

Spawn: Each pelagic egg capsule contains a single egg. The capsules are similar in shape and transparency to those of *Nodilittorina millegrana*. They differ, however, in having four tiers (three rings) and being larger, averaging 0.25 mm in diameter and 0.15 mm in height. The area containing the zygote averaged 0.11 mm in diameter.

Early development: In culture dishes, veligers hatched within about 24 h after isolation of uncleaved ova (averaging 0.07 mm in diameter). The newly hatched veligers averaged 0.11 mm long and had an operculum but lacked eyes. The veligers remained alive for 5 d, at which time they still lacked eyes, but the shell length had increased to 0.13 mm.

Family PLANAXIDAE

Planaxis sulcatus (Born, 1780)

Habitat: A wide-ranging component of the chthamalid–*Tetraclita* (midlittoral) zones on pebble and slab substrata.

Specimens examined: 409 averaging 15.8 mm long (range, 8.7–21.6) from May 1982 through November 1983 for state of reproduction; 139 specimens 7.5–13.9 mm long for minimum size of sexual maturity.

Sex ratio: 1.0 male:1.2 female.

Reproduction and early development: This species is ovoviviparous with a brood chamber at the termination of the pallial oviduct in the dorsal head-foot (RISBEC, 1935; THORSON, 1940). During December and through March, neither the males nor females had gametes. The gonads were reduced in size but retained the coloration of dark-orange to rust-colored testes and cream ovaries characteristic of the reproductive period.

Beginning in April, males with sperm in the vas deferens and some females with ova (0.12 mm in diameter) in the oviduct appeared, and gametes were present in some individuals of both sexes through November. From May through October, the brood chamber was filled with stages of development from uncleaved zygotes (average diameter, 0.12 mm) within a membrane to free (*i.e.,* not enclosed in a membrane) veligers lacking eyes but having an operculum and averaging 0.13 mm long. In most cases, the contents of the brood chamber were uniform in that only one developmental stage, or closely sequential stages, were present. In a few cases, the brood chamber contained uncleaved ova and a few free veligers, indicating that the brood chamber is filled following the release of veligers. When the brood chamber was filled, the oviduct usually contained ova. The major period of reproduction, based on the occurrence of a majority of mature individuals and brooding females, is from June through September.

The smallest male, based on gonad coloration, was 8.7 mm long, and sperm were present in the vas deferens. The smallest female with a cream-colored ovary was 9.6 mm long, the smallest with ova in the oviduct 10.0 mm long, and the smallest with the brood chamber occupied was 10.3 mm long.

Comments: RISBEC (1935) described the reproduction of *Planaxis sulcatus* from New Caledonia and THORSON (1940) did so from Bushire, Iran, Persian Gulf. The entire process described by Risbec and Thorson (through the free veliger stage, including the lack of eyes in hatched veligers) and the process found in specimens from the Jordan Gulf of Aqaba are essentially the same. However, the suppression of the pelagic larval stage and the development of the veligers into small snails in the brood chamber found by Thorson in the Persian Gulf was not found in the Gulf of Aqaba.

Both RISBEC (1935) and THORSON (1940) reported a low number of males compared to females. Based on this finding, and coupled with not having seen *Planaxis sulcatus* copulating, Thorson proposed parthenogenetic development. *Planaxis sulcatus* lacks a penis; actual sperm transfer was not observed in this study, nor is the mechanism known. Clustering, however, is a common pattern of behavior during submergence and emergence. The cluster may include a large number of individuals; in one case a total of 867 specimens were counted in one cluster. In another case a 1:1 male to female ratio was found within a cluster (compare with the above 1.0:1.2 ratio). MAGNUS & HAACKER (1968) attributed the clustering behavior of *P. sulcatus* to physical factors, including prevention of

drying during exposure and protection against wave action. It is proposed herein that another aspect of clustering is the transfer of sperm, probably during submergence.

Based on the above, parthenogenetic development, as proposed by THORSON (1940), is considered unlikely. The high female to male sex ratio found by RISBEC (1935) and THORSON is considered a sampling problem. My experience is that a skewed sample with respect to sex in this and other species with an approximate 1:1 ratio is not uncommon. This is especially the case in small-sized samples.

Family CERITHIIDAE

Cerithium caeruleum Sowerby, 1855

Habitat: This is the largest of the cerithiids occurring in the intertidal zone. It usually occurs between the two cerithiids described below, from above to below the *Tetraclita* (midlittoral) zone on smooth fossil reef bottoms and other slab having a sand cover.

Specimens examined: 416 averaging 27.3 mm long (range, 14.0–34.2) from August 1982 through May 1984 for reproductive state; 101 specimens 10.0 to 23.0 mm long for minimum size of sexual maturity.

Sex ratio: Distinction between male and female can only be made when gametes are present. For 161 with gametes, the sex ratio was 1.0 male:0.6 female.

Reproduction: Males with sperm in the vas deferens were found from January through September but most commonly from February through August. Females with ova in the oviduct were present from April through September but most commonly from April through August. The latter period is considered to be the major period of reproduction. The smallest male, based on the presence of sperm, was 17.3 mm long, and the smallest female having ova was 20.2 mm long.

The actual process of sperm transfer was not observed. Pairing was observed frequently in the field and laboratory and was similar to that of *Cerithium muscarum* Say, 1832, described by HOUBRICK (1973).

Spawn: Specimens kept in aquaria from mid-April through early June deposited egg masses on the aquarium sides as well as on pebbles and clumps of algae during the day and night on 27 of 54 days. The deposition was not related to a particular lunar or tidal cycle. The masses were typically pale yellow in color and arranged in a continuous linear series of tight folds or loops up to 4 mm high and 50 mm long. The arm of the folds was 0.4 to 0.5 mm thick. The individual capsules suspended in a gelatinous matrix averaged 0.15 mm in diameter, and the contained zygote was 0.09 mm in diameter.

Early development: Within 5 to 6 d following deposition of egg masses, veligers, averaging 0.14 mm long, hatched. The veligers were kept alive for 4 d after hatching and did not develop eyes.

Clypeomorus bifasciata (Sowerby, 1855)

Nomenclature: According to Dr. R. S. Houbrick (personal communication), this species is probably the same as *Clypeomorus morus* (Bruguière, 1792) reported by MASTALLER (1979).

Habitat: Characteristic of the chthamalid (midlittoral) zone and is the highest occurring of the three intertidal cerithiids.

Specimens examined: 332 averaging 15.9 mm long (range, 9.8–20.5) from June 1982 through May 1984, except August 1982, for state of reproduction; 51 specimens 9.0–13.0 mm long for minimum size of sexual maturity.

Sex ratio: The sexes could be determined only when gametes were present; for 179 specimens, the ratio was 1.0 male:1.4 female.

Reproduction: Some males with sperm in the vas deferens were found each month except December 1982 and 1983 and February 1983. Ovigerous females were absent or least abundant from September through February–March and most common from April through August. The latter period is considered as the major period of reproduction. Both the smallest male with sperm in the vas deferens and the smallest female with ova in the oviduct were 9.2 mm long.

Spawn: In an aquarium, *Clypeomorus bifasciata* deposited white egg masses on the underside of clumps of the alga *Enteromorpha.* The masses were usually 2–3 mm wide, variable in length, and the mass had an irregular shape. The individual capsules within the gelatinous mass were aligned in rows perpendicular to the width. The capsules averaged 0.13 mm in diameter, and the contained zygote was 0.08 mm in diameter.

Early development: Hatching of eyed veligers occurred 3–4 d after egg mass deposition and were 0.13–0.14 mm long. They were kept alive for 10 d following hatching and no significant morphological changes occurred.

Clypeomorus petrosa gennesi
(Fisher & Vignal, 1901)

Nomenclature: According to Dr. R. S. Houbrick (personal communication), this taxon is synonymous with *Clypeomorus tuberculatus* (Linnaeus, 1758) reported by MASTALLER (1979).

Habitat: Occurs below the *Tetraclita* (midlittoral) zone, most commonly in depressions with sand occurring in the fossil reef substratum.

Specimens examined: 287 averaging 20.2 mm long (range, 14.2–24.5) from June 1982 through March 1984 for state of reproduction; 105 specimens 7.8–19.1 mm long for minimum size with gametes.

Sex ratio: 1.0 male:0.5 female based on 201 specimens with gametes.

Reproduction: Males with sperm in the vas deferens were found during each month except December 1982 and January 1983. Females with ova in the oviduct were most common from May through September; some ovigerous females with few ova were found in April and from October through January. The major period of reproduction is considered to be from May through September. The smallest male with sperm in the vas deferens was 14.4 mm long, the smallest ovigerous female 15.8 mm long.

Pairing was observed on numerous occasions in the field and laboratory but actual sperm transfer was not; pairing was essentially the same as noted above for *Cerithium caeruleum*.

Spawn: In an aquarium, deposition of yellowish egg masses occurred on the underside of *Enteromorpha* clumps or, in the absence of algae, on the sides of the aquarium. The sand and detritus covered masses were a continuous string 2–3 mm wide and with individual capsules suspended in a gelatinous matrix. The capsules averaged 0.13 mm in diameter, the zygotes 0.09 mm in diameter.

Early development: Veligers with eyes hatched 5 d after deposition and averaged 0.13 mm long. The veligers remained alive for 1 wk and no significant morphological changes occurred.

Class Gastropoda, subclass Pulmonata

Family Siphonaridae

Siphonaria laciniosa Linnaeus, 1758

Nomenclature: According to Barash & Danin (1972), *Siphonaria laciniosa* and *S. kurracheensis* Reeve, 1856, are synonymous.

Habitat: Most common in the chthamalid zone and between the *Tetraclita* and chthamalid (midlittoral) zones. In the absence of a recognizable chthamalid zone, it occurs most commonly above the *Tetraclita* zone.

Specimens examined: 245 from March 1983 through May 1984 averaging 14.0 mm long (range, 9.1–22.2).

Reproduction: The presence of gametes was determined by teasing apart the gonad (ovotestis) and the hermaphroditic duct. Sperm were present every month except July, August, and September, whereas the presence of ova was restricted to December through May, being most abundant from January through March. The latter period is considered the major period of reproduction.

During the major period of reproduction, the gonad was bright yellow and reached a maximum size of 3.2 mm wide × 5.2 mm long. By contrast, when ova were absent, the gonad was burnt orange and greatly reduced in size, the minimum being 0.8 mm wide × 1.6 mm long.

Actual copulation was not observed but behavior similar to that reported for *Siphonaria japonica* (Donovan, 1824) by Hirano & Inaba (1980) was observed.

Spawn: *Siphonaria laciniosa* deposits benthic egg ribbons. The ribbons were typically dome-shaped, yellowish, and coated externally with sand. The shape of the ribbon varied from a "C" to a loose coil and ranged in size from 1.2 mm wide × 10 mm long to 1.8 × 54 mm. Larger ribbons were seen in the field but not measured. Capsules containing the zygote were suspended within the ribbon, were ovate in shape, and averaged 0.17 mm wide × 0.23 mm long.

The deposition of ribbons in the field and laboratory lasted from early January to late April. In the field, the ribbons were deposited on exposed surfaces, coated with sand, and exposed to the air during spring ebb tides. Deposition was not related to a particular lunar or tidal cycle but occurred only at night. The latter is consistent with other behaviors of *Siphonaria laciniosa*, which is a homing species active only after sunset and when submerged (Hulings, 1985).

Early development: Hatching of operculate but eyeless veligers occurred about 10 d after deposition. Eyes appeared within 2 to 3 days. The hatched veligers averaged 0.18 mm long (range, 0.17–0.19) and remained alive for 2 wk, during which no obvious morphological changes occurred.

Comments: Thorson (1940) reported two siphonarians from the Persian Gulf, *Siphonaria kurracheensis* (=*S. laciniosa*) and *S. sipho* Sowerby. The descriptions of the shape, size, and color of the egg ribbon, the size and shape of the egg capsule, and the embryological development and hatching reported for *S. sipho* by Thorson are almost identical to those of *S. laciniosa* from the Jordan Gulf of Aqaba. In addition, Thorson reported direct development in *S. kurracheensis* (=*S. laciniosa*), *i.e.*, the veliger stage was completed in the capsule and at hatching, crawling juveniles emerged. This is in contrast to the hatching of veligers in *S. laciniosa* in the northern Gulf of Aqaba.

Class Bivalvia

Family Mytilidae

Brachidontes variabilis (Krauss, 1848)

Habitat: Most characteristic between the chthamalid and *Tetraclita* (midlittoral) zones or in the middle midlittoral (Safriel *et al.*, 1980). This species typically occurs as dense beds in depressed areas of beach rock or fossil reef.

Specimens examined: 247 from October 1982 through May 1984 averaging 19.5 mm long (range, 12.8–27.3).

Sex ratio: 1.0 male:0.8 female.

Reproduction: The gonads penetrate into the mantle. The coloration of the mantle lobe containing the ovaries is typically reddish, although variable in shade, and that containing the testes is cream colored. Gametes were present in at least some if not all of the specimens of both sexes each month. In addition, at least some individuals of both sexes had enlarged gonads each month.

Comments: WILSON & HODGKIN (1967) found spawning of *B. variabilis* in Western Australia to be restricted to March–April although they noted that spawning probably continued throughout the summer. They found in *B. variabilis,* compared to other mytilids, significant differences in the time of year and the length of spawning, as well as the beginning of gametogenesis and the presence of a "reproductively neutral phase."

Family OSTREIDAE

Ostrea forskali Chemnitz, 1785

Nomenclature: According to MASTALLER (1979), *Ostrea cucullata* Born, 1780, is synonymous with *O. forskali.* The former species has been variously placed in *Saccostrea* (BRALEY, 1982), *Crassostrea* (FAO, 1972), or *Lopha* (MASTALLER, 1978).

Habitat: Characteristic of the *Tetraclita* (midlittoral) zone.

Specimens examined: 144 averaging 39 mm long (range, 19–62) from April 1982 through June 1983.

Sex ratio: 1.0 male:2.6 female based on 43 specimens with gametes.

Reproduction: Ovigerous females occurred from June through November and in January. The greatest abundance occurred from July through October–November. Males with sperm were found from June through October. The major period of reproduction is considered to be from July through October–November. The possibility of hermaphroditism in *Ostrea forskali* was not investigated.

Comments: FAO (1972) found the greatest density of spat occurred during December–January, although *Ostrea forskali* spat were often absent or in the minority compared to those of other oysters. BRALEY (1982) reported low level and continuous reproduction in *O. forskali* with, however, peaks in November–December, March–April, and late June. He also found no correlation between reproduction and temperature, and a planktonic larval life of 3–4 wk.

DISCUSSION

Various aspects of the reproduction of 15 dominant species of mollusks from the rocky intertidal zone along the Jordanian coast of the Gulf of Aqaba have been investigated. The species range in vertical distribution from the supralittoral fringe to the lower midlittoral.

The fauna can be divided into continuous reproducers (*i.e.,* those that reproduce the year round) and restricted reproducers, with periods of reproduction being indicated by the majority of specimens having ova in the oviduct and sperm in the vas deferens or similar structures at the same time. The continuous reproducers include *Cellana radiata, Monodonta dama, Nerita forskalii, Nerita polita, Littorina scabra scabra* (probable), *Nodilittorina millegrana,* and *Brachidontes variabilis.* The restricted reproducers include *Acanthopleura haddoni, Nodilittorina subnodosa, Planaxis sulcatus, Cerithium caeruleum, Clypeomorus bifasciata, Clypeomorus petrosa gennesi, Siphonaria laciniosa,* and *Ostrea forskali.* Cycles within the continuous reproducers may exist; in addition, there may be longer or shorter periods of reproduction within the restricted reproducers. For example, among the latter group, there were often specimens with or without gametes in the ducts at the beginning and end of the major period of reproduction. There were also species in which sperm were present before and after the presence of ova (*P. sulcatus, C. caeruleum, C. bifasciata, C. petrosa gennesi,* and *S. laciniosa*). An investigation of gametogenesis (in progress) may provide additional information on the above and other aspects of reproductive periodicity.

The temporal patterns of reproduction noted above are not related to tide level or a species' vertical position in the intertidal zone. For example, the highest species in the supralittoral fringe, *Nodilittorina subnodosa,* had a restricted period of reproduction, while the next highest, *N. millegrana,* reproduced the year round. The supralittoral fringe–upper midlittoral *Littorina scabra scabra* is assumed to reproduce continuously. Within the midlittoral, both continuous and restricted reproducers were found.

Water temperature in the northern Gulf of Aqaba has a narrow annual range, 20 to 27°C, whereas average annual air temperature has a much wider range, 16 to 32°C. Among the species investigated there was no direct relationship between temperature and reproduction or spawning in the continuous reproducers. They reproduced and spawned throughout the annual range in air and water temperature. Among the restricted reproducers, 7 out of 8 of the species reproduced when annual water and air temperatures were warmer (generally May through October). In two species (*Cerithium caeruleum* and *Clypeomorus bifasciata*), however, reproduction in April coincided with a 4°C increase in annual air temperature but little increase in water temperature. The other restricted reproducer, *Siphonaria laciniosa,* reproduced during the coldest period of annual air and water temperatures. Thus, the pattern of the relationship between reproduction or spawning and temperature is highly variable. If there is a relationship, as seems to be the case for some species, air temperature, having a wide range, may be more significant than water temperature, having a narrow range. And as noted previously, the terrestrial environment exerts greater influence on the intertidal zone of Jordan than the marine environment.

Vertical migration of most of the mobile species occurs with the change in sea level, from high during December–May to low during July–October (Hulings, unpublished data). The continuous reproducers, including the sessile *Brachidontes variabilis,* reproduced irrespective of changes in sea level. Among the restricted reproducers, including the sessile *Ostrea forskali,* all reproduced during lowered sea level except *Siphonaria laciniosa.* The latter, a permanent homer and non-migrant (Hulings, 1985), reproduced during the period of higher sea level, a period during which the egg ribbons were submerged more often than exposed.

There was no consistent pattern between tide level or vertical position and type of spawning except in species of the supralittoral fringe. Both *Nodilittorina millegrana* and *N. subnodosa* deposited pelagic egg capsules. *Littorina scabra scabra,* transitional between the supralittoral fringe and the upper midlittoral, brooded and hatched veligers. Within the midlittoral, a wide variety of spawning patterns occurred.

The absence of a relationship between reproduction (or spawning) and tidal levels and lunar cycles may result from the tidal levels and lunar cycles being out of phase. In addition, the annual changes in sea level modify the tide levels. Hulings (1985) found that activity patterns in *Cellana radiata* and *Siphonaria laciniosa* were not related to tidal level (except that these animals are active only when submerged) or lunar cycles.

The hatching of veligers occurred before, during, and after the relatively short periods of primary productivity, as well as during the extended period of oligotrophic conditions. Hatching occurred up to 7 d following deposition of the spawn, and the resulting veligers were small, less than 0.20 mm in length. It appears that the length of veliger life is short, based on their small size and the generally low primary productivity in the area.

Indirect development is characteristic of all the species, based on direct observation or literature sources. Development through, and hatching of, veligers was observed in all species except *Acanthopleura haddoni, Cellana radiata, Brachidontes variabilis,* and *Ostrea forskali.* Among the veligers were those with, without, or developing eyes prior to or after hatching. Veligers with eyes prior to hatching included those of *Nerita forskalii, N. polita, Clypeomorus bifasciata,* and *C. petrosa gennesi.* Those lacking eyes prior to and up to 1 wk following hatching included *Monodonta dama, Littorina scabra scabra, Nodilittorina millegrana, N. subnodosa, Planaxis sulcatus,* and *Cerithium caeruleum.* The veligers of *Siphonaria laciniosa* developed eyes 2 to 3 d after hatching. The significance of the presence or absence of eyes in the veligers at hatching is not known.

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NOTE ADDED IN PROOF:

Too late for inclusion in the text, information has been obtained on the reproduction of another intertidal gastropod from the Jordan Gulf of Aqaba.

Nerita undata Linnaeus, 1758

(Family Neritidae)

Habitat: Only two specimens found, both on boulders above the *Tetraclita* (midlittoral) zone. Mastaller (1979) reported finding only one specimen.

Specimens examined: One female 19.8 mm long, October 1982; one female 28.0 mm, August 1985.

Reproduction: No spermatophores like those in *Nerita forskalii* and *N. polita* nor any other type were found.

Spawn: The female collected in August 1985 was kept in a seawater table with continuously circulating water. In September 1985 the specimen deposited 11 egg capsules near to and just under the base of a permanently submerged pebble. The capsules are white and composed of mostly round spherulites averaging 0.07 mm in diameter (range, 0.05–0.08). The shape of the capsules is more elliptical than round, averaging 2.7 mm wide × 3.5 mm long (range, 2.4–4.0).

Early development: Development from uncleaved ova to veligers with eyes and opercula occurred in about 3 w. The capsules contained an average of 76 larvae (range, 70–85); the veligers averaged 0.34 mm long. Hatching occurred about 4 w after deposition of the capsules.